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COMPLEX MAGNETIC FIELDS ENABLE STATIC MAGNETIC FIELD CUE USE FOR RATS IN RADIAL MAZE TASKS

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Male Wistar rats were trained in an eight-arm radial maze task (two sessions per day, delayed-non-matching-to-sample) that included an intramaze static magnetic field "cue" (185 μT) specific to the entrance point of one of the arms. Rats were exposed daily for 60 min to a complex magnetic field waveform (theta-burst pattern, 200–500 nT), presented with several different interstimulus intervals (ISIs), either immediately following training sessions or immediately preceding testing sessions. Application of the theta-burst stimulus with a 4000 ms ISI significantly improved the rats' memory for the arm of the radial maze whose position was indicated by the presence of a static magnetic field cue. Reference memory errors were homogenously distributed among all eight arms of the maze for sham-exposed rats, and among the other seven arms of the maze for complex magnetic field-treated rats. These results suggest that static magnetic field cues may be salient orienting cues even in a microenvironment such as a radial maze, but their use as a cue during maze learning in rats is dependent on whole-body application of a specific time-varying complex magnetic field.

Keywords complex magnetic fields, cues, magnetic field, rat, spatial navigation

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The biological effects evoked by physiologically relevant "complex" magnetic field waveforms are a function of their spatio-temporal properties. For instance, the authors (McKay et al., 2000) have shown that the consolidation of background contextual cues during fear learning was markedly reduced by 30 min post-learning applications of a 500 nT complex theta-burst patterned (100 Hz bursts embedded in a theta (7 Hz) rhythm) magnetic field but consolidation was not affected by a different complex magnetic field or intensity-matched sinusoidal fields. Similarly, Martin et al. (2003) have rigorously identified the specific waveform patterns, inter-stimulus and intra-stimulus frequencies, durations, and intensities necessary to evoke robust analgesia. Together the waveform specificity and application timing specificity data for magnetic field modulation of memory and analgesia, and a host of other experimental preparations for both human and animal models, strongly suggest that specific aspects of behavior may be changed by magnetic fields with specific spatial structures applied at the appropriate temporal interval.

For some species, environmental exposures to weak intensity and time-varying magnetic fields from geomagnetic sources can modulate behavior, particularly navigation-directed behaviors (Southern, 1971; Keeton et al., 1974). Within an experimental setting, Kimchi and Terkel (2001) have reported that blind mole rats, which naturally inhabit subterranean environments, can efficiently complete a maze task using the ambient static geomagnetic field for orientation. Changing the magnetic environment in which the task was performed markedly diminished this efficiency. As the authors have shown the radial maze to be of great utility for addressing the effects of complex magnetic fields (McKay & Persinger, 2000), and because they have shown that specific behaviors can be modified in rodents by the correct tuning of the spatio-temporal parameters of the applied field, the authors decided to integrate these successes and test the possibility that complex magnetic fields might modulate static-magnetic field-based navigation in the Wistar rat.

Because Wistar rats are not known "static geomagnetic field sensors," and because the intensity gradient of the ambient static geomagnetic field over the surface of the authors' radial maze is essentially zero, they optimized their procedure by strategically inserting a static magnetic field "cue" that might serve as a marker for the entrance point to one of the eight arms of the maze. This article examines the capacity for male Wistar rats to detect this artificial cue and make use of it for solving a maze task. Furthermore, the article examines the use of extremely low frequency complex magnetic fields to modify this process. It reports that a theta-burst patterned complex magnetic field waveform presented at a specific inter-stimulus interval facili-

tated the consolidation of the location of the static magnetic field cue and enabled the rat to use it later for solving the maze task.

METHOD

Subjects

A total of 44 male Wistar rats served as subjects. Animals were obtained from Charles River (Quebec, Canada) when they were about 60 days old and were 4 to 7 months old at the time of testing. Rats had been housed (2–3 per cage) in standard colony conditions. Ambient temperature was maintained at 20 ± 1°C with 12-h photophase onset at 0730 hours local time. Prior to the experiment rats were given food and water ad libitum. Motivation to learn the maze was mediated by a moderate food deprivation schedule equivalent to one-hour ad libitum feeding per day; maze training and post-training food presentation took place during the early photophase. All procedures were approved by the Laurentian University Animal Care Committee, in accordance with the guidelines established by the Canadian Council for Animal Care (CCAC). The experiments were completed over a 1-year period.

Procedure

Radial Maze with Arm-Specific Static Magnetic Field Cue. The maze consisted of a 60-cm wide (octagonal) arena with eight 90-cm long by 10-cm wide arms radiating outward from each of the eight sides of the central arena (after Olton & Samuelson, 1976). The maze was elevated 1-meter above the floor by a 4-legged wooden-topped table positioned directly beneath the central arena. The maze was situated in a room containing numerous visuospatial cues including shelving, tables, and chairs.

The arms of the maze were numbered one through eight, beginning with the eastern-most arm and proceeding clockwise. Prior to the experiment one table leg had been magnetized and positioned directly beneath the entrance to the arm numbered seven. The amplitude (intensity) of the static magnetic field of the table leg was approximately 400 μT (4 Gauss) (GM1A Micropower Gaussmeter with a PA-70 Probe [maximum resolution given instrument drift, 1 μT], Applied Magnetics Laboratory, Baltimore, MID). The intensity of the static magnetic field present at the surface of the radial maze was measured with a FM 300 Vector Fluxgate Magnetometer (resolution to 1 nT; maximum resultant value = 175,000 nT). This instrument was set to measure resultant

values (the vector sum of the X, Y, and Z components of the static magnetic field). The straight-line distances connecting the center of the maze (30 cm from each arm entrance) to a point 20 cm into each arm, and the straight-line distances connecting the center of the maze to the midpoint between each arm (30 cm) were measured with the FM 300 magnetometer in linear 1-cm increments (51 measurements per arm, 30 measurements per inter-arm region, 648 total measurements). A small region immediately above the source of the static magnetic field was quantified with the Micropower Gaussmeter, as the intensity exceeded the ceiling measure of the FM 300 magnetometer.

Cluster analysis, operating on the 648 intensity data points as individual cases, was employed to statistically verify that an empirically real intensity "cue" existed. A "high intensity" cluster was generated and consisted of 13 points (all 185 μT) in a quasi-spherical distribution eleven centimeters from the straight-line distance to the entrance to arm seven. The remaining 635 data points could be considered relatively "lower" intensity (mean 54.5 μT, SD = 16.4 μT). One centimeter adjacent to the anomaly the static field dropped to 110 μT, and over the next few centimeters quickly attenuated to background levels (Figure 1). The mean static magnetic field intensity over the entire surface of the maze was 57.0 μT (SD = 23.4 μT).

Maze Paradigm and Treatment Conditions. For ten sequential days animals were pretrained in a two session per day delayed non-matching-to-sample radial maze paradigm. Each day consisted of an initial training session followed two hours later by a testing session. The first pretraining day consisted only of a single 15-min session wherein rats were allowed to freely explore the maze environment. During the training sessions all eight arms of the radial maze were associated with reward (approximately 100 mg piece of rat chow per arm). Each rat was allowed to forage throughout the maze to obtain any four reinforcements. Removal occurred immediately before any additional arms were entered. During the testing session (2 h later) rats were returned to the maze and were appetitively rewarded for entering the four arms not entered during the training session.

Throughout the 2 h inter-session intervals rats were singly housed in the treatment room containing the equipment used to generate the patterned magnetic fields. The coils consisted of two large (112 cm by 125 cm) aluminum racks each wrapped around their perimeters by 72 turns of 30 gauge (AWG) copper wire (total 13 cm wide). The rats were placed in polycarbonate cages on shelves within the racks. Each coil was connected to a custom-constructed digital-to-analog converter that transformed a computer waveform file (a series

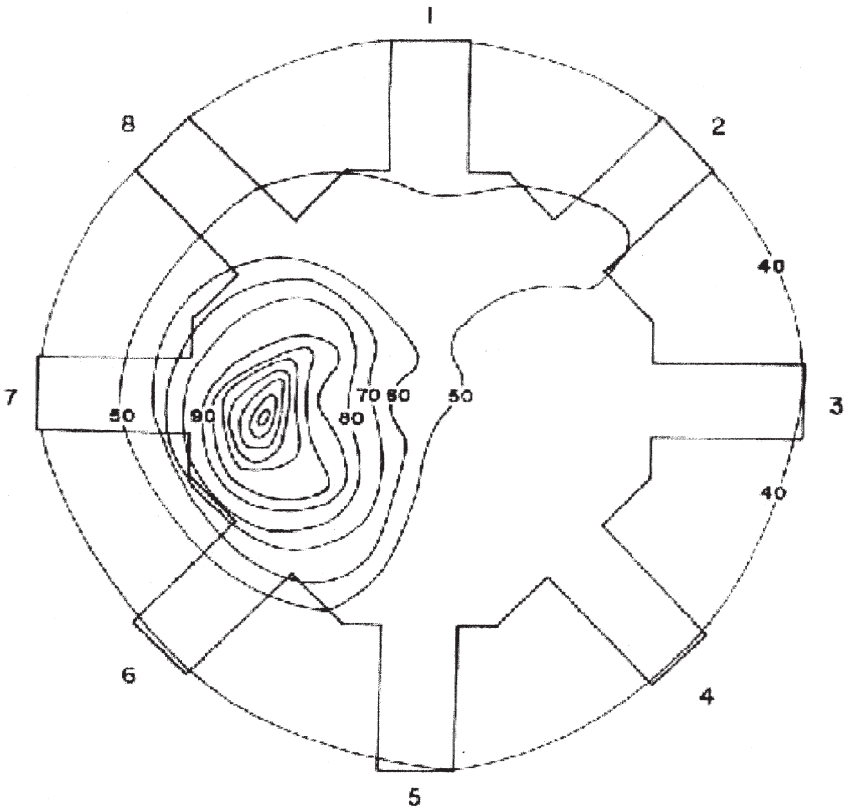

Figure 1. Isointensity contour map of the static magnetic field within the radial maze.

of values between 0 and 255, where 128 is neutral polarity and values less than and greater than 128 are negative and positive polarity, respectively) into a voltage equivalent (–5V to +5V). A plot of the magnitude of the values against their sequential order in the waveform file graphically depicted the shape of the complex waveform. For the present experiment the waveform utilized was one that had been shown to elicit long-term potentiation (LTP) in hippocampal slices when applied directly (Rose et al., 1988) and whose efficacy in modulating memory has been established in the present authors' previous work. This pattern consisted of a priming pulse followed 170 ms later by 4 pulses at 100 Hz (e.g., theta bursting). For our application the pattern had been programmed into the software as a series of 22.4 values between 128 and 255 (Figure 2) and thus was converted from 0V to 5V by the digital to analog converter. The pixel duration (the length of time the

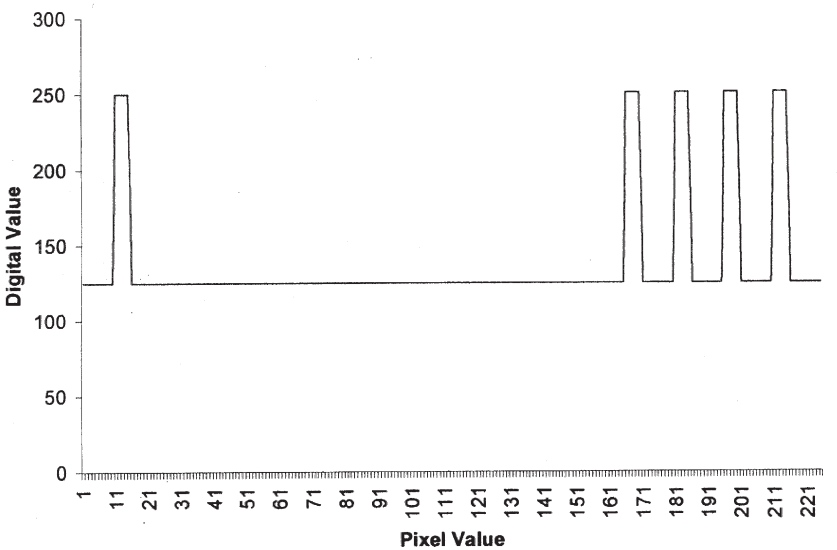

Figure 2. Temporal pattern of the theta-burst complex magnetic field stimulus. The time between the first "priming" pulse and the cluster "burst" of pulses was 170 ms (theta rhythm). Interstimulus times between the four pulses within the burst was 10 ms (100 Hz).

software sent individual values to the digital to analog converter) was set at 1 ms to maintain the temporal parameters of theta bursting. The voltage changes associated with the waveform were sufficient to produce magnetic fields varying from 200 nT to 500 nT (measured) at the location of the animals within the coils. Throughout the pretraining period the computer equipment was activated but the coils were disconnected from the digital-to-analog converter (stray magnetic fields within the coils from 60 Hz sources were below measurable limits (<10 nT)).

Subsequent to ten days of task familiarization rats were given an additional ten sequential days of training that included complex magnetic field treatments between the two daily radial maze sessions. Following each of the initial daily training sessions rats were immediately exposed to the complex magnetic fields (200–500 nT) for 1 h (Immediate Group; $N = 16$), exposed to the complex magnetic fields (200–500 nT) for 1 h after a 1-h delay (Delayed Group; $N = 16$), or received sham exposures (<10 nT) in the inactivated coil (Sham Group; $N = 12$). During the first experiment ($N = 28$) the waveform was presented at inter-stimulus intervals of 0 ms, 1 ms, 2000 ms, 4000 ms,

and 10,000 ms treatment days 1 through 5 (one ISI per day), respectively, and in the same successive order on treatment days 6 through 10, respectively. Each application of the complex magnetic field pattern was defined as one stimulus presentation. During the second experiment (N = 16) the optimal inter-stimulus intervals for modulating memory of the location of the static magnetic field cue as determined in experiment I (ISIs = 4000 and 10,000 ms, see Results) were chosen as key ISIs. Possible windows of efficacy (±500 ms) were then pursued around these optimal ISIs to ascertain the specificity of these inter-stimulus increments. The resulting inter-stimulus intervals employed during experiment II were 3500 ms, 4000 ms, 4500 ms, 9500 ms, and 10,000 ms on treatment days 1 through 5, respectively, and the same successive order was employed on treatment days 6 through 10, respectively.

Removal of Possible Olfactory and Light Wavelength Confounds. The role of navigation-relevant olfactory cues has been ruled out for visuo-spatial radial maze paradigms (Rawlins & Deacon, 1993), and is not considered a contributing (confounding) component to the map-sense utilized in navigation based on static magnetic field cues (Gould, 1998). However, to be rigorous the authors endeavored to minimize any olfactory contribution to the experiments by thoroughly wiping the floor of the maze before and after each animal was tested with a dilute (0.4%) solution of acetic acid, thereby generating an essentially homogeneous olfactory environment.

Several investigators have addressed the role of ambient light in modulating the transduction of Earth-strength static magnetic fields for the purpose of navigation (Leask, 1977; Semm et al., 1984; Semm & Demaine, 1986; Lohmann, 1993; Lohmann & Lohmann, 1996; Deutschlander et al., 1999; Deutschlander et al., 1999), and synthetic static magnetic fields in the context of the biological efficacy of low intensity time-varying magnetic fields (Prato et al., 1997; Prato et al., 2000). The effect of ambient light appears to be wavelength dependent (Phillips & Borland, 1992; Wiltschko et al., 1993), and depending on the task the wavelength of light can either abolish the ability to respond to the static magnetic field or lead to a distortion in the interpretation of the meaning of the static magnetic field (Phillips & Borland, 1994). To minimize this confound in the present study the authors employed a full spectrum fluorescent light source in both the maze room and the complex magnetic field exposure room. This strategy results in species-typical behaviors (Phillips & Borland, 1992; Wiltschko et al., 1993; Phillips &d Borland, 1994).

Analyses. Reference errors, defined as arm entries during the testing sessions that had been reinforced 2 h earlier during training sessions, were recorded for each arm of the maze for each day of testing; the overall number of reference errors per day was also computed for each rat. To accommodate the contribution of individual variability to reference error commissions, a reference error ratio was computed for each of the 10 days of the study that included post-training or pre-testing exposures to the magnetic fields. The error ratio for each day was calculated as the daily number of reference errors divided by the mean of the last 3 days of the pretraining baseline. Errors into specific arms were left untransformed.

Multivariate analysis of variance (MANOVA) was the primary statistical tool. Unless stated otherwise, the configuration of these MANOVAs were two repeated levels (2 blocks of 5 ISIs per block) and one non-repeated level (treatment group). Correlated *t*-tests and Student Newman-Keuls ($p < .05$) were employed as post hocs where appropriate. All analyses were completed using SPSS software operating on a VAX 4000 computer.

RESULTS

Experiment I

A learning curve (decreased commissions of reference memory errors across sessions) was evident during the pretraining period [$F(8,200 = 3.45, p < .01$], and did not differ significantly between treatment designations [$F(2,25) = 0.13$, ns]. During the testing (magnetic field application) component of the study a statistically significant difference in the ratio of reference memory errors committed on a daily basis (daily errors normalized to baseline errors) was noted between treatment groups [$F(2,25) = 3.48, p < .05$]. Post hoc analysis indicated that rats given 60 min applications of the complex magnetic field immediately after the training sessions committed relatively more reference memory errors per day (relative to baseline) (mean = 0.88, SEM = 0.14) than did rats in the delayed group (mean = 0.54, SEM = 0.08) or rats in the sham group (mean = 0.52, SEM = 0.06). These latter two groups did not differ significantly from one another. Statistically significant interactions between treatment group and block of training, and between treatment group and ISI, were not evident (all Fs < l.76, ns) (Figure 3).

To discern the effects of presenting the theta-burst patterned stimulus at specific ISIs for the memory of each of the individual arms of the maze the

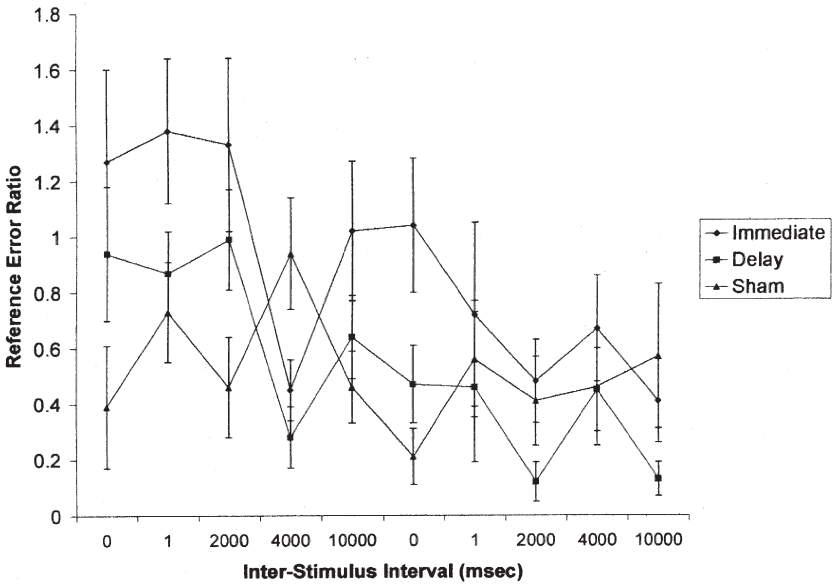

Figure 3. Daily mean relative reference errors (±SEM) during testing sessions for rats exposed to sham conditions or immediate or delayed magnetic field applications of one of five interstimulus intervals of the theta-burst patterned complex magnetic field.

authors employed 8 "arm-specific" MANOVAs. Only the MANOVA assessing the static magnetic field-cued arm reported a statistically significant interaction between treatment group and ISI for numbers of reference memory errors committed into that arm [$F(8,100) = 3.34$, $p < .01$, $\text{eta}^2 = 0.21$]. Post hoc analysis indicated that those rats in the immediate and delayed groups (which did not differ significantly from one another) committed significantly fewer errors into the cued arm than did sham exposed rats following exposure to the theta-burst patterned magnetic fields applied with either 4000 ms or 10,000 ms ISIs and was robust across both treatment blocks (Table 1). The authors' finding cannot be attributed to a treatment-induced aversion to this arm as the total number of entries into the cued arm (irrespective of their designation as appropriate arm entries or reference memory errors) did not differ between treatment groups as a function of ISI [$F(8,100) = 1.09$, $p > .05$]. Differences between the groups for each of the radial maze arms during the nine day pretraining (treatment-free) period were not evident.

Table 1. Mean numbers of reference memory errors (average of two applications of each ISI) into the static magnetic field-cued arm of the radial maze for rats given sham treatment or applications of complex magnetic fields for 60 min immediately following training sessions or for 60 min immediately preceding testing sessions

		ISI = 4000 ms		ISI = 10000 ms	
	N	Mean	SEM	Mean	SEM
Experiment I					
Sham	6	0.67[a]	0.21	0.50[c]	0.22
Immediate	11	0.18[b]	0.12	0.00[d]	0.00
Delayed	11	0.00[b]	0.00	0.00[d]	0.00
Experiment II					
Sham	6	0.33	0.21	0.00	0.00
Immediate	5	0.00	0.00	0.20	0.20
Delayed	5	0.00	0.00	0.00	0.00

[a] vs. [b]post hoc $p < .01$ and [c] vs. [d] post hoc $p < .001$.

Experiment II: Effective ISI Windows

A progressive decrease in the commissions of reference memory errors was evident throughout pretraining [$F(8,104) = 2.20$, $p < .05$]; the pattern of this learning curve did not differ significantly between groups [$F(2,13) = 0.19$, ns]. During the testing sessions wherein rats received applications of the theta-burst patterned magnetic field stimuli, those rats in the immediate field application group committed relatively more reference memory errors per day (relative to baseline) (mean = 0.89, SEM = 0.14) than did those rats in the delayed group (mean = 0.50, SEM = 0.13) or the sham-exposed group (mean = 0.64, SEM = 0.07). This difference was just above the threshold for statistical significance [$F(2, 13) = 2.78$, $p < .10$] (Figure 4).

Again the ISI-evoked modulation of arm-specific memory was assessed with eight separate MANOVAs. Unlike the first experiment, the interaction between treatment group and ISI was not statistically significant [$F(8,52) = 1.01$, $p < .05$] but this finding was expected given that the ISIs had putatively been optimized for the current experiment. Arm-specific differences in reference error commissions were not apparent for any of the other seven arms of the maze. Serial one-way analyses of variance were utilized to examine the direction of group differences for the five optimized ISIs. Although the criterion for alpha of $p < .05$ was not reached for any of the five inter-stimulus

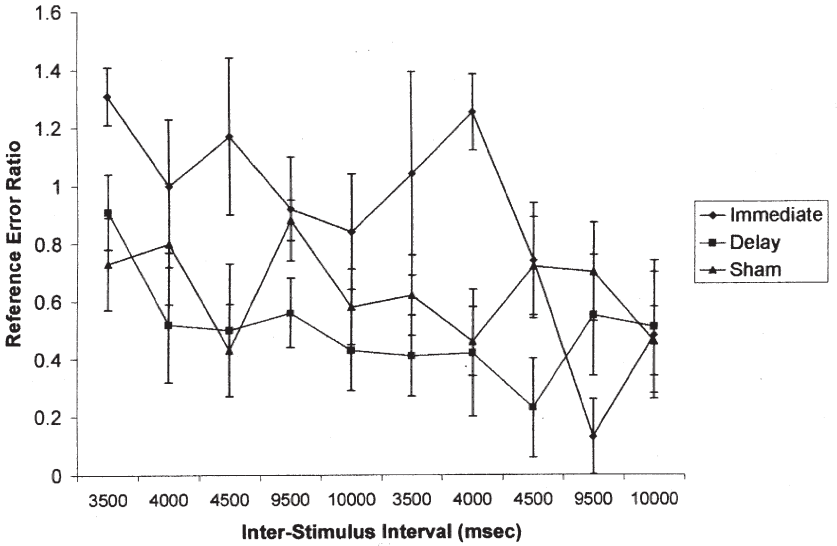

Figure 4. Daily mean relative reference errors (±SEM) during testing sessions for rats exposed to sham conditions or immediate or delayed magnetic field applications of one of five inter stimulus intervals of the theta-burst patterned complex magnetic field.

intervals the effect size (approximately 25% of the variance) and direction of effect for the 4000 ms inter-stimulus interval was identical to that revealed in experiment I (Table 1). These differences would likely have reach statistical significance with a larger sample size (e.g., commensurate with the *N* of experiment I). The significant effect for the 10,000 ms ISI from experiment I was not replicated. Differences between the groups for each of the radial maze arms during the 9-day pretraining (treatment-free) period were not evident. Only a qualitative reproduction of the results of experiment I may be rooted in the inverse relationship between the intensity of the ambient geomagnetic activity and the magnitude of the difference (for several dependent measures) between sham-exposed (e.g., environmentally exposed) and synthetically treated rats (McKay & Persinger, 1999, 2003). The ambient time-varying geomagnetic field differed on average by several nanoTesla between replicates of the experiments. Additionally, Prato et al. (1995) have shown that the biological efficacy of a time-varying (sinusoidal) field may be a function of the amplitude (intensity) of the static magnetic field on which it is superimposed. Such variability in results between replicates of experiments is not uncommon in bioelectromagnetic research, suggesting that even under

highly controlled experimental conditions the nuances of subtle ambient geomagnetic changes may potently affect the outcomes of synthetic treatments.

Magnetic Cue Traversals and Subsequent Cue Use (Experiments I and II Combined)

Discerning the intrinsic relationship between the static magnetic field cue and the finding that theta-burst patterned complex magnetic fields at specific ISIs reduced commissions of reference errors into the static magnetic field-cued arm required selecting only those rats that entered this arm during the training session. These rats had thus traversed the cue, and by definition, a reference memory error during the testing session was possible. Consequently, the disconcordance among commissions of reference memory errors during the testing session was analyzed as a function of the treatment received during the inter-session interval. Experiments I and II were combined for these analyses.

Chi-squared analyses indicated that there were no disconcordances among the treatment groups for entering or not entering the static magnetic field-cued arm during training sessions (the maze session prior to theta-burst magnetic field exposure) for both the 4000 ms ISI days [$\chi^2(2) = 2.38$, $p > .05$] and the 10,000 ms ISI days [$\chi^2(2) = 2.97$, $p > .05$]. However, there was significant disconcordance from chance expectancy among the immediate, delayed, and sham groups for committing or not committing a reference memory error into the static magnetic field-cued arm during the post theta-burst exposure (testing) session for the 4000 ms ISI days [$\chi^2(2) = 7.44$, $p < .05$, phi = 0.61]. Statistically significant disconcordance between treatment groups was noted for the 10,000 ms ISI days [$\chi^2(1) = 4.75$, $p < .05$, phi = .54], but only when the immediate and delayed groups were collapsed into a single group. The source of the disconcordance for both ISIs was the decreased numbers of reference memory errors for the rats receiving either the immediate or the delayed magnetic field exposure relative to sham-exposed rats.

To identify how robustly the memory of a specific arm could be facilitated given the combination of a static magnetic field cue predicting the location of the arm, and the application of a theta-burst patterned magnetic field presented at the appropriate ISI to enable the utilization of that cue, the authors compared with correlated *t*-tests the mean number of errors committed into each arm against the number of errors committed into the cued arm. In general, it was found that sham-treated rats committed equal numbers of

errors between all arms of the maze [all $t(11) < 2$, ns], whereas rats exposed to the theta-burst magnetic field pattern at either 4000 or 10,000 ms ISIs committed significantly fewer errors into the cued arm than they did into any other arm [all $t(31) > 2$, $p < .05$]. In a very limited number of cases the number of errors into the cued arm did not differ significantly from a non-adjacent arm.

Animals traversed the maze with a mean velocity of 16.9 cm/s (SEM = 0.86 cm/s), which did not differ as a function of treatment group [$F(2,41) = 1.92$, $p > .05$]. Given that the maximum change in amplitude of the static magnetic field was 75 μT per 1 cm in the vicinity of the anomaly, at a mean velocity of 16.9 cm/s an average animal would in effect experience a time-varying field with a rise time of 75 μT/0.06 s. This rate of change is equivalent to 1.3 μT/ns and is thus within the bioeffective amplitude range when considered on a neuronal (ms) timescale.

DISCUSSION

The authors have demonstrated that rats exposed to a theta-burst patterned complex magnetic field presented with a 4000 ms ISI showed a marked improvement in the recall of the spatial position of a radial maze arm whose location was indicated by the presence of a static magnetic field cue. This finding was not related to an a priori bias to this arm as rats in all treatment groups traversed the static magnetic field cue equivalent numbers of times during the pre-exposure period (training session) and reference memory errors during testing sessions for control rats were distributed homogeneously between all eight arms of the radial maze. Cumulatively, these results suggest that the location of the static magnetic field cue was consolidated into a representation (memory) of the training session environment, and available for task-specific use during the testing session, only if the rat received whole-body application of a specific complex magnetic field during the intersession period.

Weak intensity time-varying magnetic fields exert some of their effects through cholinergic or opioidergic pathways (Lai, 1996; Thomas & Persinger, 1997; Thomas et al., 1997; Thomas et al., 1998). Such a transduction mechanism would be consistent with the roles of these transmitter systems in the physiology of the neural substrates of learning and memory, particularly the hippocampus (Bramham & Sarvey, 1996; Fischer et al., 1999), and are consistent with the known effects on learning and memory from directly administering drugs that modulate these transmitter systems (Watts et al., 1981;

Spain & Newsom, 1991). Whereas these latter studies require invasive drug administration and a conventional ligand–receptor interaction, the use of a magnetic field to stimulate an endogenous receptor is noninvasive and can be described as the interaction of an endogenous receptor with a "virtual" ligand (Persinger et al., 2001).

Alternatively, magnetic field-induced memory deficits may be related to resonance-like interactions between the applied magnetic fields and the brain (Liboff, 1985; Lednev, 1991). Rose et al. (1988) determined that the optimal electrical stimulation parameters to evoke LTP in hippocampal slices consisted of a priming pulse followed 140–170 ms later by 3–5 burst pulses at 100 Hz. Arguing the principle of resonance, which suggests that any oscillating system characterized by a specific periodicity will respond in a nonlinear manner when an external stimulus with the same periodicity is applied to the system (Liboff et al., 1987), Richards et al. (1996) applied as a weak intensity magnetic pulse this optimal theta-burst pattern (the same as that employed in the present study). These authors reported that subjects given this optimal pattern accurately remembered almost twice the verbal details of a short story compared to sham-exposed controls.

Although speculative at this point, it may be that the complex magnetic fields employed in the present study, which possessed the necessary temporal parameters to effect or intercalate with endogenous memory-encoding physiological processes, may have directly influenced such processes via resonance-like interactions. This putative mechanism for magnetic field effects is consistent with the recent finding that aggregates of neurons demonstrate intrinsic firing preferences, as inferred by the enhanced response of neurons to injected current whose stimulus parameters were similar to the endogenous oscillatory neuronal parameters; weaker or zero neuronal responses were associated with stimulus parameters that did not approximate endogenous activity (Hutcheon & Yarom, 2000). Interestingly, the hippocampus exhibits the lowest threshold of any structure in the brain to respond to electrical stimulation (John, 1967) thus providing a suitable target for weak intensity magnetic field stimulation. In fact, weak intensity magnetic fields are known to alter electrical brain functioning as demonstrated by the entrainment of neural signals with the applied magnetic fields as measured by scalp-based electroencephalography (Persinger et al., 1997). ELF-evoked neural modulation has also been demonstrated with electrodes chronically implanted into the cortex (Vorobyov et al., 1998), or into the hippocampus (Jenrow et al., 1998). Collectively these data support the possibility of neuroelectrical modulation by exogenously applied theta-burst magnetic fields.

One possible outcome of the application of a magnetic field pattern with the correct spatial and temporal geometry is the modification (potentiation or depotentiation) of the set of synapses normally recruited into task-specific memory consolidation. The consolidated representation of the environment and the veridical parameters of the environment could either be incongruent and discerned behaviorally as a deficit in accurate recollection, or the representation might be augmented and discerned behaviorally as enhanced recollection. The vector of this change would be determined by the exact spatiotemporal properties of the applied field relative to the endogenous neuromagnetic signals, and would be conceptually defined by the principles underlying the constructive interference and destructive interference of waves in classical physics. Support for this line of reasoning is based on the reports of Bawin et al. (1996) and Jenrow et al. (1998) who showed in hippocampal slices that ELF magnetic fields directly modulated the electrical activity of those cells implicated in learning and memory processes. That the present authors were able in the same study to demonstrate the facilitation of one component of memory (arm-specific recall of the static magnetic field cue) yet inhibition of a different component of memory (the general impairment in memory for all rats exposed to the theta-burst magnetic field immediately following training sessions) may further suggest region-specific interactions of the magnetic fields within brain space. For example, consider that the exact regions of the hippocampal complex underlying learning and memory processes differ between tasks, as noted by the requirement of the dorsal hippocampus for spatial memory, and the ventral hippocampus for contextual memory (Moser et al., 1995; Richmond et al., 1999).

An alternative, or perhaps complementary, explanation to resonance-like interactions is the transduction of the time-varying magnetic fields by biogenic magnetite, a putative peripheral mechanism of static magnetic field detection (Kirschvink & Gould, 1981). In several species, especially those with migratory behaviors, one component of the multi-coordinate map sense is based on a sensory magnetic map whose information is resolved from latitude-dependent static geomagnetic field intensity (equator to poles: 30,000 nT to 50,000 nT) (Gould, 1980; Moore, 1980). Magnetite has been confirmed in a myriad of phylogenetically diverse species (Blakemore, 1975; Gould, 1978; Walcott et al., 1979; Mather & Baker, 1981; Zoeger et al., 1981; Beason & Nichols, 1984; Walker et al., 1988; Kirschvink et al., 1992; Brassart et al., 1999) and its role in sensing Earth-strength magnetic fields (usually for the purpose of navigation) has been discerned by a variety of techniques (Wiltschko & Wiltschko, 1972; Walcott & Green, 1974; Semm &

Beason, 1990; Walker et al., 1997; Wiltschko et al., 1998). Magnetite-dependent sensory neurons respond to changes in magnetic field intensity with a change in the firing frequency of the associated neuron (Walker et al., 1997). Moreover, the role of biogenic magnetite in sampling the magnetic field for route-based navigation has been demonstrated in a variety of rodent species (Mather & Baker, 1981; Burda et al., 1990; Marhold et al., 1997), and in fact the magnetite is localized within the anterior head region of rodents in comparable amounts to that found in pigeons (Walcott et al., 1979). The recent elucidation that magnetite is present within the biological system as chains (Diebel et al., 2000) and directly connected to the central nervous system supports previous calculations by Mann et al. (1988) that such a configuration would enable the torque of static magnetic fields on magnetite particles to be linearly summed together, thereby overcoming thermal noise (kT) constraints necessary to activate the proposed mechanosensitive transmembrane ion channels (Kirschvink et al., 1992).

The finding that an intramaze static magnetic field cue was effectively utilized by rats treated with a specific complex magnetic field, but not other complex magnetic fields or by rats exposed to sham conditions, might suggest a vestigial static magnetic field detection process whose information value is potentiated to a level of salience sufficient for detection or consolidation by the specific complex magnetic field. Interestingly, the ophthalmic branch of the trigeminal nerve (or its homologous equivalent) appears to mediate the neural link between the peripherally located magnetite and the central nervous system (Semm & Beason, 1990; Walker et al., 1997; Diebel et al., 2000). The ophthalmic branch of the trigeminal nerve projects to the ventral posteromedial thalamus (VPM) (Parent, 1996) and then somatotopically to the primary somesthetic cortex of the parietal lobe, a cortical region associated with spatial representations of the environment (Kolb & Whishaw, 1996).

The strong connections between thalamus and hippocampus, or thalamus via the cortex and hippocampus, may thus link the external static magnetic field cue detection process with an internal maplike representation. Because (1) the electrophysiological parameters of all thalamic cells (Steriade & Deschenes, 1984) satisfy the endogenous oscillation and synchrony requirements (Jenrow et al., 1998) for optimal coupling between neural structures and applied magnetic fields, and (2) spindle oscillations within the thalamus occur with interspindle frequencies of 6–7 Hz (e.g., approximately 140–170 ms between spindles) every 3 to 30 s (Von Krosigk et al., 1993) or 0.1 to 0.2 Hz (Steriade & Deschenes, 1984), the 4000 and 10,000 ms ISIs in the present study may

possess the necessary temporal parameters to directly intercalate with the thalamic component of the detection process and thus allude to a possible resonant-like interaction between the time-varying fields and the thalamic activity. Moreover, the role of neuromagnetic synchronization as a correlate of perception has recently been elucidated (Srinivasan et al., 1999). Therefore magnetic field entrainment (or augmentation) of endogenous thalamic oscillations, known to be associated with memory-specific dynamic stabilization of synapses (Kavanau, 1996), may have enabled the incorporation of the within-maze static magnetic field cue into the memory of the environment by the Wistar rat via a process that may otherwise be electrically sub-threshold (vestigial).

Interestingly, copious deposits of biogenic magnetite are found within the human brain and particularly high levels have been measured within the hippocampus (Kirschvink et al., 1992); lesser concentrations have been reported for homogenized rat brains (Pardoe & Dobson, 1999), although concentrations specific to the hippocampus have not been reported. Reports describing one way or the other the role of hippocampal magnetite in static magnetic field detection have not been published. However, the hippocampus does appear to function as a spatial map (O'Keefe & Nadel, 1978). The purported cellular basis of this map is hippocampal place cells, neurons whose activity is exclusive to specific spatial geometries (O'Keefe & Burgess, 1996). Because place-cells encode discrete components of the environment, if they were functionally coupled to magnetite the hippocampus might function as both a static magnetic field detector and the spatial map representing the location of the differing intensities in the intramaze static magnetic field. The activity of hippocampal place cells shows high task-specific fidelity during periods of post-training memory consolidation (Louie & Wilson, 2001), the period wherein the present authors applied complex magnetic field treatments. It is well established that the strength of the memory for a hippocampal-dependent tasks is positively correlated with the magnitude of long-term potentiation within hippocampal synapses (Maren et al., 1994). By reinforcing the electrical patterns at these synapses with frequency-matched external stimuli it may be that the specific set of synapses encoding the representation of one specific arm with its static magnetic field cue may have been reinforced, in this case to a level of salience where it could be further utilized during testing sessions to enhance the recollection of a previously entered arm.

The authors have interpreted the changes in commissions of reference memory errors for complex magnetic field-treated rats in the context of a change in some aspect of spatial memory processing. However, the possibil-

ity emerges that the treatment effect in the present study might reflect magnetic field-evoked changes in the sensory salience of the static magnetic field cue, or alternatively an evoked change in the orienting response of the rats. The former possibility might be addressed experimentally with rats after removing all spatial cues from the radial maze room, leaving only the static magnetic field cue. By employing multiple intensities of the static magnetic field cue the intensity threshold for detection in untreated (sham-exposed) rats might be compared to the intensity threshold for detection in treated (complex magnetic field-exposed) rats. If the sensory salience of the cue for the rats was affected, one would predict a higher intensity threshold for detection in sham-exposed rats, and a markedly reduced intensity threshold for complex magnetic field-treated rats.

A synthesis of the results presented suggests an interaction between the mechanisms of static magnetic field detection and time-varying magnetic field detection. Thus application of the appropriate magnetic field may facilitate the detection of natural sources of sudden changes in the static magnetic field, including buried materials such as mineral deposits or water. Such an interaction may underlie dowsing, a practice wherein certain individuals, using forked sticks or L-shaped rods are able to locate underground water. Rocard (1964) has reported that reliable (accurate) measurements from dowsers required the traversal of a threshold magnetic gradient of about 0.3 mG/m/s (30 nT/m/s). Presti and Pettigrew (1980), by proposing that magnetite, as a magnetic field detector, may be coupled to muscle spindles, have suggested that this mechanism of magnetoreception may be responsible for the large deflections of the hand-held instruments used by the dowsers. Given that dowsers reliably locate the anomaly approximately one meter past the anomaly (at 1 m/s) (Rocard, 1964) the present authors' results suggest that a time-dependent change in the functional state of the brain, perhaps regulated by the appropriate ambient time-varying geomagnetic perturbations, is superimposed on the peripherally mediated detection of the static magnetic field anomaly, and enables expression of the dowsing response.

To the authors' knowledge this is the first report of an experimental manipulation that augmented static magnetic field consolidation for the purpose of navigation. Previous attempts to describe magnetoreception in vertebrates have emphasized the necessary neurostructural basis of the transduction step, but have not considered the role that specific functional states may play in the ultimate manifestation of magnetoreception as an adaptive orienting cue. The consequences of geomagnetic storms, whose intensities approximate the experimentally controlled intensities incorporated in the present study

have for some time been associated with pronounced functional changes in brain activity (Petersen, 1947). The navigational accuracy of organisms as a function of geomagnetic storm conditions (above 30 nT) has been considered, but reports vary in terms of the severity of the effect (Southern, 1971; Keeton et al., 1974). In accordance with the present findings it is suggested that future studies may clarify the relationship between the time-varying (a.c.) geomagnetic field and static (d.c.) geomagnetic field-based navigation by considering the role of discrete classes of geomagnetic pulsations (which have both a frequency [temporal] component and an intensity component) rather than considering sudden storm intensity alone.

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